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THE DISTRIBUTION OF OCTOPUSES OF *GRANELEDONE* (CEPHALOPODA: OCTOPODIDAE) IN REFERENCE TO DEEP-SEA FEATURES

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ABSTRACT

Although deep-sea hydrothermal vents are renowned for having many apparently endemic taxa, normal deep-sea taxa also occur at vents. These opportunistic taxa have been hypothesized to tolerate these physiologically stressful habitats due to pre-adaptation to low oxygen conditions. Octopuses of the deep-sea genus *Graneledone*, likely a monophyletic group, appear to be one such taxon as they occur at several East Pacific hydrothermal vents. To further our knowledge of this genus and of other taxa opportunistic at chemosynthetic habitats, collection localities of these octopuses north of 40°S were verified and whether features such as vents, cold seeps, tectonic activity or hydrocarbon deposits were present near the collection localities was determined.

Hydrothermal vents, cold seeps or hydrocarbon deposits lie within one degree of 17 of the 24 localities confirmed north of 40°S. This distribution suggests that the octopuses routinely occur in low oxygen habitats, potentially due to a pre-adaptation, a hypothesis that will require a species-level phylogeny for the genus. Low oxygen habitats offer opportunists increased prey biomass and possibly reduced predation rates. In addition, several of these areas offer hard substrata essential for egg attachment and brooding by females of *Graneledone*.

Key words: *Graneledone*, deep sea, habitat use, Octopodidae, macrofaunal predators.

INTRODUCTION

Benthic octopuses of the family Octopodidae occur from the intertidal zone to depths as great as 3,931 m (Voss, 1988), but what determines the distribution and abundance of deep-sea octopuses and of other mobile deep-sea macrofauna remains unknown. Trawled specimens provide few details on habitat use and few observations of deep-sea octopuses from submersibles have been reported (e.g., Vecchione & Roper 1991). Compounding the lack of taxon-specific data is our meager knowledge of what constitutes distinct sea floor habitats. If we are unable to distinguish what the animals recognize as distinct habitats, we cannot distinguish preferential habitat use.

Hydrothermal vents, characterized by elevated temperatures, anoxic, metal-rich fluids and extremely high biological productivity, offer one distinctly recognizable deep-sea habitat. Although the vent fauna appears to be highly endemic, members of the "normal" deep-sea fauna are observed occasionally in apparent association with these habitats. Whether these are chance sightings of the animals near the vent habitat (Tunnicliffe et al., 1998), or whether these taxa actively exploit vent resources is unresolved. The ability to exploit vent resources is thought to be possible only if these non-vent specialized animals are unusually tolerant of low oxygen availability (Tunnicliffe, 1991).

This paper explores the global distribution of the octopodid genus *Graneledone*, "normal" deep-sea predators that occur on three different ridge systems and prey on vent fauna (Voight, in review). If some members of the genus exploit hydrothermal vent habitats because tolerance of low oxygen availability has evolved in the group, then other members are predicted to occur in such areas. To test this hypothesis, documented occurrences of members of the genus are compiled. For each locality, geological indicators of reduced oxygen availability are noted. Hypotheses of pre-adaptation to low oxygen cannot be assessed until the phylogeny of the genus is resolved, but recognition of a such a distributional pattern could motivate such an effort and help us distinguish deep-sea habitats. Global examinations of the distribution of other taxa that appear to be opportunists at vents may aid in determining the generality of the pattern seen here.

MATERIALS AND METHODS

The Genus

The genus *Graneledone* is argued to be monophyletic because several character states that are derived among the Octopodidae (Voight, 1997) characterize the genus in a unique combination. The nearly equal-sized papillae (also called warts or tubercles) on the skin of the dorsal mantle and head, stout papillae over each eye, comparatively few gill lamellae (6–9), the absence of the plesiomorphic ink sac and crop diverticulum, and the presence of small tubular bodies at the junction of the tube and cement gland, as illustrated for spermatophores of *G. pacifica* (Voss & Pearcy, 1990: fig. 20e, f), support the hypothesis of monophyly. Six species are currently recognized in the genus, although species distinctions are poorly defined (Voss & Pearcy, 1990; Villaneuva & Sánchez, 1993). Subtle morphological variation among North Pacific specimens collected from different depths has been detected and suggests the presence of cryptic species (Voight, 1998). With few specimens available from other areas, the potential existence of other cryptic species cannot be assessed. As a result, species names are applied here only in reference to type specimens or type localities.

Octopuses of the genus *Graneledone* can reach weights of nearly 1 kg and exceed 50 cm in total length. They have been recorded from depths as shallow as 512 m (O'Shea & Kubodera, 1996), although most range between 850 (Voss, 1988) and 2,755 m (Voss & Pearcy, 1990). Their biology remains poorly known. Reported gut contents include copepods, amphipods (Voss & Pearcy, 1990) and crabs, vent gastropods and polychaetes (Voight, in review). Reproduction among these species likely follows that typical of cephalopods, being limited to the extreme terminal portion of the life span (Boyle 1983, 1987). Females brood eggs attached to hard substrate (Voight & Grehan, in review).

Documentation of Distribution

Collection localities north of 40°S of specimens of *Graneledone* documented by museum holdings, literature reports and/or by submersible-based photographs or videotapes (Appendix 1) were compiled. Literature reports were also evaluated as a data source, although when possible, museum specimens were examined to verify generic identification. Well-illustrated taxonomic accounts by established workers (e.g., Berry, 1917; Villanueva & Sánchez, 1993) were accepted, as were recent re-determinations at the South Africa Museum (M. Roeleveld, pers. comm.) and Boyle et al.'s (1998) report of three members of *Graneledone* from the Hebrides Shelf. Two reports, however, had to be rejected. Bruun's (1945) report of the genus from Iceland remains unverified. The report lacks illustrations, and the specimen cannot be located in the collections of the Zoologisk Museum of Copenhagen (T. Schiøtte, pers. comm.). Grieg's (1933) report of the genus from Norway, cited uncritically by Stephen (1944), was also rejected. The photographs of the specimens and the measurements Grieg (1933) reported do not support the identification of these specimens as members of *Graneledone* based on criteria discussed by Thomsen (1931).

Submersible-based photographs and videotapes that showed key characters were also used to document the presence of members of the genus. If the photographs and videotapes of octopuses *in situ* clearly showed the single row of arm suckers and dorsal skin papillae that among octopodids north of 40°S at over 800 m depths are unique to members of *Graneledone* (Voss, 1988), the records were accepted. Examination of seven submersible-collected specimens from the North Pacific (Appendix 1) that were identified in videotapes and photographs as members of *Graneledone* supported their generic determination.

Habitat Characterization

A description of the sea floor geology of every documented collection locality of the genus was sought. Pertinent data, reported in Appendix 1, include the presence of hydrothermal vents or vent deposits, plate margins (where either subduction or transform movement occurs), turbidite flows (massive submarine landslides), and hydrocarbon (gas hydrate and/or petroleum) deposits. Under at least some conditions, these geological features are associated with environments rich in sulfides or methane. Bacteria mediate the oxidation of these reduced compounds and can form the basis of chemosynthetic species as-

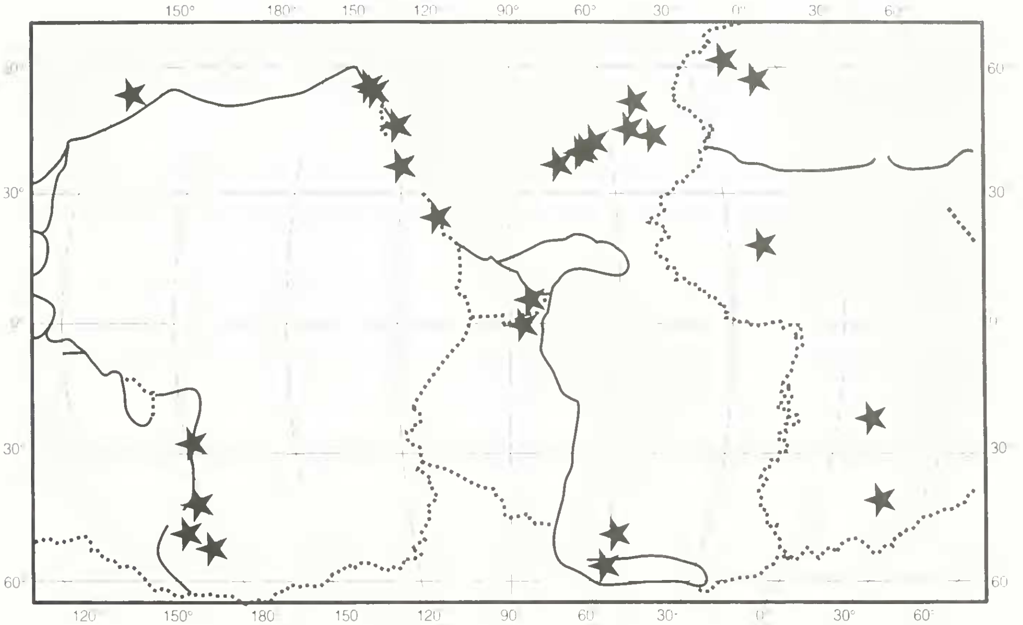

FIG. 1. The non-Antarctic collection localities of octopuses in the genus *Graneledone* documented are indicated by stars. Dotted lines indicate the position of spreading centers; solid lines indicate subduction zones. Map adapted from Baker et al. (1995).

TABLE 1. Summary of the habitat types from which octopuses of *Graneledone* have been documented. Localities are considered different if they are separated by at least one degree latitude or longitude. Of the 24 localities north of 40°S, 17 are unusual in being near a hydrothermal vent, cold seep or hydrocarbon deposit. Of the seven seemingly normal northern habitats, five are in the Atlantic Ocean (Appendix 1).

Number of different localities	Habitat type
8	Hydrothermal vents
4	Cold seeps at tectonically active areas
5	Hydrocarbon (petroleum/gas) deposits
7	Seemingly normal areas north of 40°S
7	Apparently unknown areas south of 40°S

semblages in areas with these features (Kulm et al., 1986; Kennicutt et al., 1988; Mayer et al., 1988).

Collection records of such taxa as vesicomyid bivalves that appear entirely dependent on endosymbiotic chemosynthetic bacteria (Fisher, 1995) have been used to hypothesize the existence of chemosynthesis in unknown areas (e.g., Kennicutt et al., 1989). The underlying assumption, however, is that members of these taxa do not vary in habitat use. Because variation in habitat use within the taxon *Graneledone* is being investigated here, these reports cannot contribute non-circular data to this study. Marine geology is poorly known south of 40°S, so records of the genus from this area could not be considered. As a result, several records, including the type localities of *G. antarctica, G. macrotyla*, although listed in Appendix 1, could not be detailed.

RESULTS

Verified localities of *Graneledone* (Fig. 1) and pertinent geological features that characterize the localities are summarized in Table 1;

supporting data are detailed in Appendix 1. Below is a brief review of the areas and the pertinent geological data.

Occurrences at Hydrothermal Vents

Benthic *Graneledone* are documented at eight hydrothermal vent fields on Explorer and Juan de Fuca Ridges, and Guaymas Basin and Galapagos Rift on the East Pacific Rise. A *Graneledone* was photographed on the Galapagos Rift (Corliss & Ballard, 1977: 448) among shells of chemosynthetic clams and live mussels. A specimen of *Graneledone cf. boreopacifica* collected near chemosynthetic clams at Axial Volcano on Juan de Fuca Ridge had preyed on vent gastropods and polychaete worms (Voight, in review).

On-going marine geological studies at Kermadec Ridge are documenting active hydrothermal vents (Matsumoto et al., 1997; Stoffers et al., 1999). This ridge is the type locality of *Graneledone challengeri* Hoyle, 1886.

Occurrences at or Near Cold Seeps at Plate Boundaries

Heat and pressure created by tectonic activity such as the subduction of oceanic plate can release reduced fluids that sustain chemosynthetic species assemblages at cold seeps (e.g., Kulm et al., 1986). The distribution and fauna of cold seeps are poorly documented compared to hydrothermal vents, but a published photograph shows a *Graneledone* at a tube worm cluster (Moore et al., 1990: fig. 6e) on the Oregon Subduction Zone.

Known cold seeps in Monterey Bay occur near 3,000 m depth on the Monterey Fan Valley system (Embley et al., 1990) and at three localities near 36°N, 122°W between 580–1,010 m (Barry et al., 1997). Octopuses have not been collected or reported from any of these sites. Specimens of *Graneledone,* however, are numerous between 1,100 and 1,660 m depth near a fault seaward of the Sur High at the mouth of Monterey Bay (Greene, 1990). The collection area, a zone of transform faulting (Greene, 1990), is likely to have additional, undiscovered cold seeps (Kennicutt et al., 1989) and oxygen tensions below 1.0 ml/l due to heavy upwelling (Kamykowski & Zentara, 1990) and the presence of a dysaerobic zone (Mullins et al., 1985).

Members of *Graneledone* are also known from the northwest Pacific where subduction also is linked to the presence of cold seeps. As at the Oregon margin, subduction at the Japan and the extreme southern Kuril-Kamchatka Trenches is documented to support chemosynthesis at depths greater than 3,000 m (Métivier et al., 1986; Le Pichon et al., 1987). In addition to what may be subduction-linked cold seeps, gas hydrates (frozen methane deposits) occur off Sakhalin Island in the Sea of Okhotsk (Ginsburg et al., 1993). Without citing precise localities, Nesis (1982) reports that *G. boreopacifica* occurs in the Okhotsk Sea and the Pacific Ocean northeast of Honshu. Unfortunately, there are no further data for this area.

The collection locality of a member of the genus off New Zealand (O'Shea & Kubodera, 1996) lies within two minutes longitude of a sea floor plume, interpreted as methane-rich water released in response to plate boundary processes (Lewis & Marshall, 1996).

Occurrences Near Hydrocarbon Deposits

Assemblages of chemosynthetic species, characteristic of the most extreme habitat discussed in this paper, also occur on passive continental margins (Sibuet & Olu, 1998). On the Northwest Atlantic margin, release of fluids from a 1929 slide of organic-rich sediment created extreme reducing conditions at 3,000 m depth (Mayer et al., 1988). In addition, bacterial production linked to hydrocarbon seepage on the continental shelf has been suggested to increase surface water productivity (Levy & Lee, 1988; Fader, 1991; D. Piper, pers. comm., cited by Fader, 1991). Hydrocarbon deposits occur in the Northwest Atlantic, as evidenced by: (1) bottom simulating reflectors, indicative of gas hydrates (e. g., Paull et al., 1995) that lie seaward south of Massachusetts (Fig. 2; Dillon et al., 1986); (2) salt domes and salt-cored anticlines that can be associated with petroleum deposits and cold seeps from Nova Scotia to Massachusetts (Fig. 2; Uchupi & Austin, 1979; Dillon et al., 1986; Swift, 1987); and (3) the immense Hibernia Oil Field (Fig. 2; Brown et al., 1989). In a seemingly similar geological setting, physical and chemical indicators of hydrocarbon seepage occur over broad areas of the Gulf of Mexico (Kennicutt et al., 1988; Sassen et al., 1998). The relationship between the collection localities of *G. verrucosa* and these three subsurface geological features is shown in Figure 2.

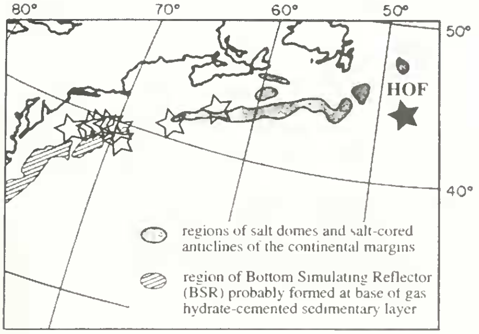
80°
70°
60°
50°
50°
40°
HOF
regions of salt domes and salt-cored anticlines of the continental margins
region of Bottom Simulating Reflector (BSR) probably formed at base of gas hydrate-cemented sedimentary layer

FIG. 2. The Northwest Atlantic collection localities of *Graneledone verrucosa* (Appendix 1) are indicated by stars. HOF indicates the position of the Hibernia Oil Field; shading represents regions of salt domes and salt-cored anticlines; cross-hatching represents Bottom Simulating Reflectors. Map adapted from Dillon et al. (1986).

Off Walvis Bay, Namibia, near the collection locality of a *Graneledone* (Villanueva & Sánchez, 1993), is the site of a turbidite flow in which about 90 km^3 of sediment created a debris flow that extends 250 km downslope (Summerhayes et al., 1979). The slide may have been initiated due to unstable gas hydrates in the sediment column (Summerhayes et al., 1979) which may contribute to vertical hydrocarbon expulsion (Hyndman & Davis, 1992). Sedimentary studies show that organic carbon is abundant locally (Embley & Morley, 1980).

Occurrences in Seemingly Normal Areas

Seven collection localities of *Graneledone* north of 40°S cannot be said to have unusual sea floor features. Some of these areas appear to be normal, such as Norfolk Canyon (Malahoff et al. 1982). Others, such as the area south of Iceland and the Gulf of Panama, appear to be virtually unexplored. Baby Bare has been closely explored. This outcrop of basement basalt is where tens of octopuses of *Graneledone* brood eggs (Mottl et al., 1998; Voight & Grehan, in review). Although warm water springs with detectable sulfide concentrations exist at Baby Bare (Mottl et al., 1998), in the immediate area of brooding neither elevated sulfide concentrations or temperatures have been detected (G. J. Massoth, pers. comm.).

South of 40°S, specimens of the genus have been collected from seven areas that appear to have received little study by marine geologists. Perhaps notable is that three specimens are from two localities directly seaward of the San Jorge Basin, a major petroleum deposit (Fitzgerald et al., 1990). In addition, upwelling off the southwest coast of Africa, may lower oxygen availability or create anoxic conditions in the area (Kamykowski & Zentara, 1990).

DISCUSSION

Octopuses of the genus *Graneledone* are documented at 31 localities around the world (Table 1, Fig. 1). Of the 24 collection localities north of 40°S, 12 are within one degree of chemosynthetic communities at hydrothermal vents or cold seeps associated with tectonic activity and five are near hydrocarbon deposits (Table 1, Appendix 1). No available data contradict the classification of seven of these localities as normal deep-sea habitats, including Baby Bare, a basalt outcrop that releases warm water with measurable concentrations of hydrogen sulfide from its summit (Mottl et al., 1998). This distribution suggests that at least some members of the deep-sea octopodid genus *Graneledone* are able to tolerate low oxygen availability. This ability may allow them to exploit resources unavailable to other taxa.

These data are robust to suggestions the submersible observations provide significant bias. Submersible-based observations are the sole source of distributional data for all hydrothermal vents, Baby Bare and Norfolk Canyon. Trawls document the presence of the octopuses in all other habitats. When localities based solely on submersible data north of 40°S are eliminated from consideration, the octopuses are still documented at ten low-oxygen areas and five normal areas. These totals are not significantly different from 17 versus 7, the totals from Table 1 (G-test, $G = 0.302$).

The large size of these octopuses is not expected to bias these results. On average, members of *Graneledone pacifica* are mid-sized among the five species of northeast Pacific deep-sea octopodids described by Voss & Pearcy (1990). Octopuses of the genus *Graneledone*, however, appear to move more slowly than do those of *Benthoctopus* and could therefore be more readily collected by trawl and submersible.

Evidence that the octopuses actually enter vent areas and therefore experience low oxygen environments at vents is three-fold. The gut of a specimen of *G. cf. boreopacifica* contained two species of vent-restricted gastropods and three taxa of vent polychaetes that the octopus ingested prior to its collection from Axial Volcano (Voight, in review). Second, a photograph from Galapagos Rift (Corliss & Ballard, 1977) shows a *Graneledone* among empty *Calyptogena* valves and live chemosynthetic mussels, the presence of which correlates with elevated hydrogen sulfide concentrations (Lutz & Vrijenhoek, 1997). The third line of evidence that these octopuses enter areas of active vents is circumstantial. Disarticulated valves of chemosynthetic clams are present up to one meter away from clam beds at North Pacific vents. Because such predators as spider crabs, galatheids and fishes are unlikely to either pick up or to prey on clams, octopuses are most likely to have entered the clam bed and removed the clams.

Even in non-low oxygen areas, their hypothesized foraging behavior may expose octopuses of the genus *Graneledone* to sulfide, a small molecule that is readily absorbed by tissues, in anoxic layers of deep-sea sediment. The distal half to two-thirds of the arms of a *Graneledone* photographed at Axial Volcano (V. Tunnicliffe, pers. comm.) and of one near Galapagos Rift (R. W. Embley, pers. comm.) were so covered with sediment that their color matched the sea floor. The octopuses may sometimes forage by probing unconsolidated sediment with their arms, which emerge covered in sediment. This presumed prey search behavior could dramatically increase the octopus' exposure to sulfide, a toxin that readily permeates cells, because it increases in concentration dramatically just under the sediment surface, especially at cold seeps and sedimented vents (Grehan & Juniper, 1996). Whether exposure of their arms to anoxic sediment through this behavior may have contributed to the evolution of reduced oxygen availability by members of this genus remains speculation.

Low oxygen environments may offer both reduced predation pressure (Fischer & Bottjer, 1995) and increased prey availability (Chevaldonné & Olu, 1996). Because hard-shelled molluscs constitute about 34% of the taxa at hydrothermal vents (Tunnicliffe et al., 1998), and octopuses of the genus *Graneledone* may be among the few deep-sea predators able to prey on them, possible advantages of entering the habitat are clear. In addition, vent and seep habitats also tend to offer exposed hard substrata. Although members of this genus occur on soft substrata, as documented by the many trawl-collected specimens and the photographs of individuals with sediment-covered arms (R. W. Embley, V. Tunnicliffe, pers. comm.), females of *Graneledone* attach and brood their eggs on hard substrata (Mottl et al., 1998; Voight & Grehan, in review). The availability of basalt at mid-ocean ridges and carbonates produced by cold seeps (e.g., Moore et al., 1990) may attract many mature octopuses (Voight & Grehan, in review).

Pre-adaptation to tolerate low-oxygen availability has been suggested to be necessary to allow "normal" deep-sea animals to enter vent habitats (Tunnicliffe, 1991). Whether octopuses of the genus *Graneledone* are pre-adapted to tolerate low oxygen environment is unknown, but these data suggest that in several geographically distinct areas, members of the genus *Graneledone* enter low oxygen habitats produced by diverse geological mechanisms. Resolution of octopodid phylogeny is required to assess the hypothesis of pre-adaptation (Voight, 1997). If, when a species-level phylogeny of the genus becomes available, taxa that occur in low oxygen habitats are monophyletic, than tolerance to low oxygen availability can be concluded to have evolved only once in the group.

More knowledge of the distribution of these deep-sea octopuses and other macrofauna that are opportunistic predators at vents may help identify the level of biological isolation of hydrothermal vents, the degree to which chemosynthetic-produced biomass is distributed to the resource-poor ocean floor and the impact of vent habitats on biota of surrounding deep-sea areas. In addition, investigations of the seemingly anomalous distributions of little-known deep-sea animals such as *Graneledone* can increase our biological knowledge of the group and help identify behaviors such as sediment-probing that may relate to evolutionary changes in their physiology.

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APPENDIX 1

Occurrences of members of *Graneledone* are listed by their habitat type, with data that characterize the habitat and how the octopuses' presence was determined. All FMNH specimens were examined. Localities separated by one degree are considered distinct. For museum specimens, the depository and catalogue number for each are reported if the data are available. (ANSP = Academy of Natural Sciences at Philadelphia; CAS = California Academy of Sciences; CMN = Canada Museum of Nature; FMNH = Field Museum of Natural History; ICM = Instituto de Ciencias del Mar, Barcelona, Spain; MNHN = Muséum National D'Histoire Naturelle, Paris; MOM = Musée Océanographique de Monaco; NSMT = National Science Museum, Tokyo; SAM = South African Museum; UMML = University of Miami Marine Laboratory; USNM = United States National Museum; ZMUC = Zoologisk Museum of Copenhagen).

Documented Occurrences at Hydrothermal vents, n = 8.

(1) EXPLORER RIDGE. 49°46′N, 130°16′W, 1,870 m. Reported by Tunnicliffe et al. (1986) as octopus identified from photograph (V. Tunnicliffe pers. comm.).

(2) JUAN DE FUCA RIDGE: MIDDLE VALLEY. 48°30′N, 128°41′W, 2,400 m; FMNH 278061; 278062; 278063; 281001; 281002.

(3) JUAN DE FUCA: ENDEAVOUR SEGMENT. 47°56–58′N, 129°08′W, 2,250 m (including Main Field, High Rise and Clam Bed vent fields). Identified from videotapes and photographs (V. Tunnicliffe, S. K. Juniper, J. Delaney, pers. comm.).

(4) JUAN DE FUCA: CO-AXIAL SEGMENT. 46°19.4′N, 129°42′W, 2,200 m. AXIAL SEAMOUNT: 45°57′N 130°01′W, 1,560 m. Identified from photographs and videotapes (V. Tunnicliffe, R. W. Embley pers. comm.); FMNH 282751.

(5) JUAN DE FUCA: CLEFT SEGMENT. 44°38–58′N, 130°15–30′W, 2,210–2,280 m. Identified from photograph (V. Tunnicliffe, pers. comm.).

(6) GUAYMAS BASIN. 27°01′N, 111°24′W, 1,996–2,000 m. Identified from photographs (V. Robigou, P. Chevaldonée, pers. comm.).

(7) GALAPAGOS RIFT: CLAM BAKE. 0°47–48′N, 86°01–14′W, 2,480 m. Identified from published photograph Corliss & Ballard (1977).

(8) KERMADEC RIDGE. Active vents occur on this ridge (Wright et al., 1998; Stoffers et al., 1999) but the region with the type locality of *Graneledone challengeri* remains a critical gap in our knowledge (Stoffers et al., 1999). *G. challengeri* Hoyle, 1886. Type locality: 29°45′S 178°11′W, 630 fm (1,175 m), Challenger Station 170A, specimen illustrated by Berry (1917). Not examined

Occurrences at or Near Cold Seeps at Tectonically Active Areas, n = 4.

(1) OREGON SUBDUCTION ZONE. Over 600 trawls systematically sampled the Cascadia and Tufts Abyssal Plains and Oregon's continental slope between 125°23.6′W and 135°22.7′W (Carney & Carey, 1982). All 29 type specimens of *Graneledone pacifica* were collected by 17 trawls between 125°13.4′W and 125°52.9′W at 1,427 to 2,755 m depth (Voss & Pearcy, 1990), a narrow area that includes the documented cold seeps (Kulm et al., 1986), areas of upwelling and the Astoria Fan (Kulm & Scheidegger, 1979). A photograph taken at 44°40′N, 125°18′W, 2,100 m shows an octopus of *Graneledone* with vestimentiferan worms (Moore et al., 1990: fig. 6e and J. C. Moore, pers. comm.). Upwelling produces large amounts of biomass which deplete oxygen through decomposition on the sea floor. The topographically complex Fan may support broader areas of chemosynthesis based on three-D perspective bathymetry map and a slope map made using SeaBeam swath bathymetry (L. Kulm, pers. comm.). Seven paratypes and 20 specimens from same area in April 1997 (FMNH 278303, 278304, 278305, 278306, 278312, 278313, 278316;

278317; 278318; 278319; 278320) were examined.

(2) MONTEREY BAY. Cold seeps are documented at 36°47.1′N, 122°2.6′W, 580-700 m; 36°44.0′N, 122°2.0′W, 875-920 m; 36°44.7′N, 122°16.6′W, 1,004 m (Barry et al., 1997); the oxygen minimum and dysaerobic zones reach these depths off Point Sur (Broenkow & Greene, 1981, cited by Mullins et al., 1985). Specimens of *Graneledone* examined: off Bodega, 4-5 mi. N on 600 fm. line (estimated 38°20′N, 123°40′W), 1,116 m, Dec. 1976; CAS 003318. 10 miles SE of N. Farallon Island, (estimated 37°45′N, 123°20′W), 1,414 m, Nov. 1950; CAS 035044. 36°40.7-41.0′N, 122°17.6-19.4′W, 1,341 m, Nov. 1975; CAS 031500. 36°29.9-30.5′N, 122°18.3′W, 1,415 m, Feb. 1985; CAS 084669. 36°29.2′N, 122°18.6′W, 1,400-1,420 m, March 1985; FMNH 286436. 36°28.3-29.3′N, 122°17.4-20.0′W, 4,409-1,384 m, Nov. 1975; CAS 031474 and 084666. 36°28.3-29.3′N, 122°17.8-03.8′W, 1,400 m, May 1985; CAS 084667. 36°15.1-15.6′N, 122°25.5-26.1′W, 1,600 m, June 1984; CAS 084665.

(3) JAPAN/KURIL TRENCH. In addition to subduction-related cold seeps associated with the Trench (Métivier et al., 1986; Le Pichon et al., 1987), ten gas hydrate deposits occur between 53°20.634′N, 144°29.206′E and 54°26.782′N, 144°04.858′E at depths of 620 and 1,040 m (Ginsburg et al. 1993). *Graneledone boreopacifica* Nesis, 1982. Type locality. 50°04′N, 151°35′E, 1,350 m, also reported from Sea of Okhotsk and the Pacific Ocean northeast of Honshu. Not examined

(4) NEW ZEALAND. Seafloor plume of methane-rich water rising over seabed at 39°58.58′S, 178°14.18′E, est. 900 m (Lewis & Marshall, 1996). 39°59′S, 178°13′E, 940-1,070 m, April 1994; NMNZ M. 118324 *Graneledone* sp. (O'Shea & Kubodera, 1996). Not examined

Occurrences Associated with hydrocarbon deposits, n = 5.

(1) NORTHWEST ATLANTIC: BOTTOM-SIMULATING REFLECTOR (Fig. 2). Fish Hawk, Blake and Albatross specimen records from Verrill (1884); station localities from Tanner (1885). 39°59′45″N, 68°54′W, 787 fm (1,464 m), 26 Aug. 1882; Fish Hawk Sta. 1123. 39°53′N, 70°35′W, 588-832 m deter. M. Vecchione (J. Moore pers. comm.); Feb. 1999. 39°50′45″N, 70°11′W, 466 fm (853 m), 1880; Blake Sta. 312. Paratype. 39°44′N, 70°28′W, 1,830-1,912 m, July 1975; USNM 730996 (reported by Villanueva & Sánchez, 1993). 39°42′50″N, 69°21′20″W, 1,050 fm (1,953 m), 1 Aug. 1883; Albatross Sta. 2050. 39°41′00″N, 69°20′20″W, 1,106 fm (2,057 m), 1 Aug. 1883; Albatross Sta. 2051. 39°34.45′N, 71°31.30′W, 466-1,255 fm (853-2,334 m), Albatross Sta. 2209, ANSP A6934. 38°44′00″N, 72°38′00″W, 1,209 fm (2,249 m), 5 Nov. 1883; Albatross Sta. 2102. 38°23′N, 73°45′W, 100-800 fm (186-1,488 m), March 1996; FMNH 281721.

(2) NORTHWEST ATLANTIC: SALT DOME/SALT-CORED ANTICLINES (Fig. 2). Blake and Albatross specimen records from Verrill (1884); station localities from Tanner (1885). 42°40′N, 62°29′ W, 1,458 m, reported by Joubin (1924); Villanueva & Sánchez (1993) likely examined and cited the same specimen as MOM 295353, collected 1913. 42°38-40′N, 63°20-43′W, 1,116-1,488 m, August 1995; FMNH 286457 n = 20. 41°33′15″N, 65°51′25″W, 810 fm (1,483 m), 1880; Blake Sta. 305. Holotype. 41°09′40″N, 66°02′20″W, 1,255 fm (2,334 m), 4 Sept. 1883; Albatross Sta. 2077. Not examined

(3) NORTHWEST ATLANTIC: HIBERNIAN OIL FIELD (Fig. 2). Collection depths of the examined specimens, below, not recorded. 45°41′N, 47°37′W, Sept. 1982; CMN 92735. 45°24′N, 48°35′W, June 1980; CMN 92734. 45°18′N, 48°35′W, Sept. 1982; CMN 92736. 45°18′N, 48° 36′W, June 1980; CMN 92522 and 92732. 45°18′N, 47°51′W, Sept. 1982; CMN 92737.

(4) NORTHWEST ATLANTIC (same petroleum reserve). 53°11.82′N, 51°56.82′W, 1,145 m, Sept. 1995; FMNH 286459.

(5) CONTINENTAL MARGIN SOUTH OF WALVIS RIDGE. 22°30′S, 12°20′E, 1,900 m. Walvis Bay Slide Scrap and high organic material in sediment (Summerhayes et al., 1979; Embley & Morley, 1980). 23°05′S, 12°41′E, 1,193 m; August 1984. *Graneledone* sp. ICM-SA 179 reported & illustrated by Villanueva & Sánchez (1993), not examined.

Specimens from seemingly normal areas north of 40°S, n = 7.

(1) SOUTH OF ICELAND. Water column surveys found no indication of active hydrothermal vents near 63°05′N, 24°25-35′W (German et al. 1994). *Graneledone:* 62°10.8′N, 19°36′W, 2,150 m, July 1903; ZMUC 20-11-1903. Examined.

(2) HEBRIDES SHELF. Large petroleum deposits at 60°N (Parnell et al. 1998). Three

specimens of *Graneledone* 55–59°N (ca. 8–15°W) depths of 900 to 1,400 m reported by Boyle et al. (1998) but not examined. Boyle et al. (1998) perpetuate Griegg's (1933) statement that members of the genus are "not uncommon" off the coasts of Norway by citing Stephen's (1944) uncritical mention of the account.

(3) NORFOLK CANYON. 37°N, 74°30′W (Upper Norfolk Canyon and Continental slope north of Norfolk Canyon) ca. 1100 m. Photographs from ALVIN dives 807 and 808 R. W. Embley, pers. comm.). No evidence of unusual biological activity (Malahoff et al. 1982).

(4) CAPE VERDE BASIN. Area of mass sediment movements (Kidd et al. 1987) that are apparently of unknown origin. *Graneledone:* 20°33′N, 18°35′W, 2,003 m, Feb. 1991; MNHN 2013. Examined.

(5) SOUTHEAST ATLANTIC. 34°S, 17°E, 1,211 m, 22 July 1903; SAM 2734. 34°S, 17°E, 1,027–1,284 m, 17 Sept. 1903; SAM 2735. 34°21′S, 17°47′E, 900–1,500 m, 17 April 1982; SAM S807. 34°16′S, 17°29′E, 1,150 m, 11 Jan 1995; SAM S3569. (Determinations relayed by M. Roelveld, pers. comm.).

(6) BABY BARE BASEMENT BASALT OUT CROP. 47°42.64′N, 127°47.15′W, 2,591 m (Mottl et al., 1998). Although warm water with detectable sulfide concentrations is released from Baby Bare, areas in which octopuses occur have normal temperatures and sulfide has not been detected (G. J. Massoth, pers. comm.). FMNH 282750.

(7) GULF OF PANAMA. Reports of specimens of *Graneledone* from the Gulf of Panama had been undocumented because specimens were severely damaged and/or poorly preserved (Hoyle, 1904; Voss, 1988). 07°15′N, 79°36′W, 1,020 fm (1,890 m), March 1891; Albatross Sta. 3393: *Graneledone* sp. reported by Hoyle (1904), not examined. 07°11–12.5′N, 79°16–18.5′W, 1,463–1,984 m, Jan. 1972; UMML 31.2484. Examination of a spermatophore in this lot supported the late G. L. Voss' identification of the material as *Graneledone* n. sp.

Records from south of 40°S which lack marine geological data and are unconfirmed, n = 7.

NEW ZEALAND.

(1) 43°9′S, 177°49′E, 780 m. Reported by Kubodera & Okutani 1994.

(2) 45°21.1′S, 173°35.8′E, 1,386 m, Oct. 1979; NZOI Stn. S153. Reported by O'Shea & Kubodera (1996).

(3) 48°15.5′S, 179°48.5′E, 512 m, Nov. 1975; FSFRL EI 259. 48°27.30′S, 179°27.56′E, 565–599 m, Nov. 1993; NMNZ M. 117874. Both reported by O'Shea & Kubodera (1996). 48°40′S, 179°51′E, 732 m, Nov. 1983 (also reported as 48°40′S, 179°1′E); NSMT Mo67835 as *G.* sp. b. 48°48′S, 179°16′E, 725 m, Nov. 1983 (also reported as 48°48′S, 179°6′E); NSMT Mo67836 as *G.* sp. b. Both reported by Kubodera & Okutani (1994).

SOUTH AMERICA—both South American records of the genus are reported by Kubodera & Okutani (1994) from directly seaward of the petroleum-rich San Jorge Basin, positioned between 45°S, 71°W and 47°S, 65.5°W (Fitzgerald et al. 1990). Offshore geology apparently unknown.

(4) 45°44′S, 59°46′W, 858 m, Oct. 1984; NSMT Mo67838 as *G. macrotyla* and NSMT Mo67837 as *G.* sp. A.

(5) 47°00′S, 59°37′W, 972 m, Oct. 1984; NSMT Mo67839 as *G. macrotyla.*

ANTARCTICA.

(6) 54°43′S, 55°30′W 1,647–2,044 m, 14 March 1966. *Graneledone macrotyla* type locality (Voss 1976).

(7) 74°05.6′S, 175°05.2′W, 2,341 m, 8 Feb. 1968. *Graneledone antarctica* type locality (Voss 1976).